Reproduction in Gag *(Mycteroperca microlepis)* (Pisces: Serranidae) in the Eastern Gulf of Mexico and the Consequences of Fishing Spawning Aggregations

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Abstract

Spatial and temporal spawning patterns of gag *(Mycteroperca microlepis)* in the eastern Gulf of Mexico were investigated by: (1) offshore cruises to suspected spawning sites; (2) interviews with grouper fishers; (3) the analysis of gag gonads; and (4) the analysis of daily incremental growth in juvenile gag otolfes. The gag spawning season extends from early February to late April, but the majority of spawning occurs in March. Spawning aggregations in the eastern Gulf are concentrated along the 80-m isobath in the area south of Apalachicola to west of Tampa, Florida. Sex-size-frequency data from gag collection in 1991, 1992 and 1993 indicated several changes in population structure

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compared with sex-size data collected by other investigators before the 1980s. The comparisons indicated that the present population shows a reduction in: (1) the average size of females; (2) the average size of males; and (3) the proportion of males (from about 17% to <2%). An increase in fishing pressure on gag spawning aggregations during the 1980s and observations by other investigators strongly suggest that a fishing selection for males during the spawning season is in large part responsible for the observed changes in the gag population. Probable mechanisms are discussed to explain the fishing-induced suppression of compensatory sex-change in these protogynous hermaphrodites.

Resumen

Patrones de desove espacial y temporal del cuna aguají (Mycteroperca microlepis) *en el este del Golfo de México fueron investigadas por: (1) cruceros mar afuera y sitios donde se sospechaba que ocurrían desoves; (2) entrevistas con pescadores de mero; (3) análisis de gonadas del cuna aguají; (4) análisis de crecimiento usando incrementos diarios en otolitos de juveniles. La temporada de desove se extiende de inicios de Febrero a fines de Abril, pero la mayoría de los desoves ocurren en Marzo. Agregaciones de desovadores en el este del Golfo se concentran a lo largo de la isobata de 80 m en el área sur de Apalachicola, al oeste de Tampa, Florida. Los datos de frecuencia de tallas por sexo del cuna aguají fueron colectados en 1991, 1992 y 1993, indicando varios cambios en la estructura de la población cuando fueron comparados con datos de talla por sexo colectados por otros investigadores antes de los 1980s. Las comparaciones indicaron que la población actual muestra una reducción en: (1) el tamaño promedio de las hembras; (2) el tamaño promedio de machos; y (3) la proporción de machos (de cerca de 17% a <2%). Un incremento en la presión de pesca sobre las agregaciones de desovadores del cuna aguají en los 1980s y observaciones efectuadas por otros investigadores sugieren fuertemente que la selección de pesca sobre los machos durante la estación de desove es en gran parte responsable de los cambios observados en la población. Se discuten probables mecanismos para explicar la supresión inducida por la pesca del cambio de sexo compensatorio en estos hemafroditas protogíneos.*

Introduction

The shallow water groupers (Family Serranidae), including gag (*Mycteroperca microlepis*), black grouper (*M. bonaci*), scamp (*M. phenax*), and red grouper (*Epinephelus morio*), support major commercial and recreational fisheries in the southeastern United States (Huntsman and Waters 1987; Bullock and Smith 1991) (see also Collins et al., this vol.). In the Gulf of Mexico, red groupers rank first among reef fish species in mean annual harvest (4.5 million kg). Gag are ranked seventh, at 1.15 million kg, but should probably be ranked second, with annual landings of about 2 million kg because fishers often misidentify gag as black grouper, resulting in landing reports that grossly underestimate catches of gag (Eklund 1993; Koenig, pers. comm.).

All species of groupers examined have proven to be protogynous hermaphrodites (Shapiro 1987), in which males result from sex change of mature females. The reproductive mode that a species exhibits may

have significant population-level consequences when that species is subject to exploitation. For instance, Bannerot (1984) and Bannerot et al. (1987), using fishery simulation models, concluded that protogynous hermaphrodites may be more susceptible to overexploitation than gonochorists (separate sexes) if fishing pressure served to reduce the normal proportion of males in the population. A significantly depressed male:female ratio could potentially restrict reproductive capacity and ultimately result in population declines.

The primary objective of this study was to define precisely the timing and location of gag spawning in the Gulf of Mexico and to gain insight into the nature of the gag mating system. Because we noted a significant decline in the number of males occurring in our samples relative to samples taken by other investigators over a decade ago, we compare historical and recent sex-ratio and size-frequency data for Gulf and Atlantic populations of gag against a background of information on temporal and

spatial reproductive patterns. We explain observed sex and size changes in gag populations in the context of known patterns and mechanisms of sex change in other species and of recent documented increases in fishing effort and landings, particularly on spawning aggregations.

Materials and Methods

Spatial and temporal spawning patterns of gag were investigated by the analysis of gonads collected by Florida State University (FSU) researchers over a two-year period (1991 through 1992). Data obtained for each gonad included size of fish (mm total length, TL) and collection date, location and depth (m). Cooperation from commercial fishers of northwest Florida was essential to this study. Data collected independently by the National Marine Fisheries Service (NMFS), Panama City Laboratory, in 1991, 1992 and 1993 were used for comparisons of sex ratio and size-frequency distributions.

Samples were collected year-round in 1991 (N = 991) before we were aware of the location of spawning aggregations. We obtained gonads from fish houses and from recreational and commercial fishers operating in relatively shallow waters (< 40 m) primarily in the area between and south of Apalachicola and St. Marks, Florida.

Samples were collected in 1992 (N = 536) from January through August in both shallow water sites (<40 m, 30% of samples) and offshore spawning sites (50 - 120 m, 70% of samples). The shallow-water samples collected in 1992 were from the same general area as those collected in 1991.

Samples from spawning aggregations were collected by hook-and-line, mostly in the area to the north and west of the Middle Grounds (southeast of Apalachicola) between the 40 and 120 m isobaths, but some samples were taken from the same depth range to the southwest of the Middle Grounds. These gonads came from catches taken by five commercial fishers who, because they derive a significant portion of their annual income from fishing the gag spawning aggregations, would give general locations of capture, including depth, but would not release exact locations. We chartered four trips with commercial fishers to spawning sites during the peak spawning period (discussed below).

Both historical and recent data sets are comparable in terms of fishing method and the geographical areas of coverage. The historical Gulf data (Hood and Schlieder 1992) were collected primarily from hook-and-line commercial fishers operating in the area of the Middle Grounds (R. Schlieder, pers. comm.), but also from recreational fishers. The historical Atlantic data (Collins et al. 1987) was collected by the same methods in various depths of water off South Carolina.

Gonad analysis

Gonads collected both years were used to determine spawning season, depth and location and to determine size-frequency distributions. Only gonads from 1992 were used to determine sex, size at sexual maturity, spawning patterns and sex ratios. Gonads were removed from freshly killed fish and either immediately placed on ice and brought back to the laboratory where they were frozen or they were preserved in Davidson's solution. All frozen gonads were thawed and weighed to the nearest 0.1 g.

Gonadosomatic indices (GSI), used to identify spatial and temporal variation in reproductive states, were calculated using the following equation:

GSI = 100(ovary weight/total body weight)

Conversions of lengths to weights were made using the following equation from Bullock and Smith (1991):

$$W = 2.680 \times 10^{-8} SL^{2.958}$$

where W = weight in kg and SL = standard length in mm.

Sex was determined microscopically for both the FSU- and NMFS-collected specimens because gross examination was unreliable. Freshly frozen ripe gonads were adequate for identifying sex and for staging oocyte development, whereas histological sections were required for identifying pre- or postspawning individuals and staging.

Frozen gonads were examined by preparing squashes, in which a bit of thawed tissue was squashed between two microscope slides and then covered with a cover slip. Each squash was examined under a compound microscope for sex, stages of oocyte development (see Moe 1969), range of oocyte size per stage, and presence or absence of late-stage atresia, if possible. Whenever sex was questionable, quick hematoxylin and eosin stains of new squashes were made, following Link (1980). This method also facilitated identification of transitionals (= individuals in the process of changing sex from female to male). The presence of live sperm in thawed testes confirmed reproductive activity.

Preserved gonads were sectioned at 10 μm, mounted on slides, and stained with hematoxylin and eosin. Oocytes were examined for stage and degree of development following Moe (1969). Fish were considered immature if the gonads were small, extremely compact, and contained oogonia, stage 1 and small stage 2 oocytes. Gonads were considered ripe if they contained stage 3 or more advanced oocytes.

Inactive fish (mature, nonreproductive), which could be identified reliably only by histological examination, contained stages 1 and 2 oocytes which were loosely held in a stroma or showed evidence of the early stages of oocyte degeneration; the gonadal wall (tunica) was typically thick, indicating, but not confirming, prior spawning activity. Individuals so classified may or may not have spawned before in their lifetime. Postspawning individuals could be identified histologically by the presence of early stage degeneration of vitellogenic oocytes or postovulatory follicles.

Landings data

Gag landings data for the Gulf coast of Florida were obtained from the Marine Fisheries Information System of the Florida Marine Research Institute, Department of Environmental Protection, St. Petersburg, Florida. A problem with the gag landings data is that gag catches are commonly recorded as black grouper. It is well known, however, that black groupers (*M. bonaci*) are rare on the west coast of Florida north of the Florida Keys (Bullock and Smith 1991). Therefore, to estimate the actual gag landings, we combined gag with black grouper landings data, but excluded Monroe County (Florida Keys) landings from our estimates.

Results

Spawning season, depth, location and pattern

GSIs of gonads collected in 1991 were low throughout the year, but suggested that gags were reproductively active from December through mid-May (Fig. 1a). GSIs of gonads collected in 1992 (most from spawning aggregations) clearly indicated that gags were reproductively active from February through April, with peak spawning from mid-February through March, followed by a gradual decline from late March through April (Fig. 1b). These spawning times were corroborated by the analysis of juvenile otolith daily increments from
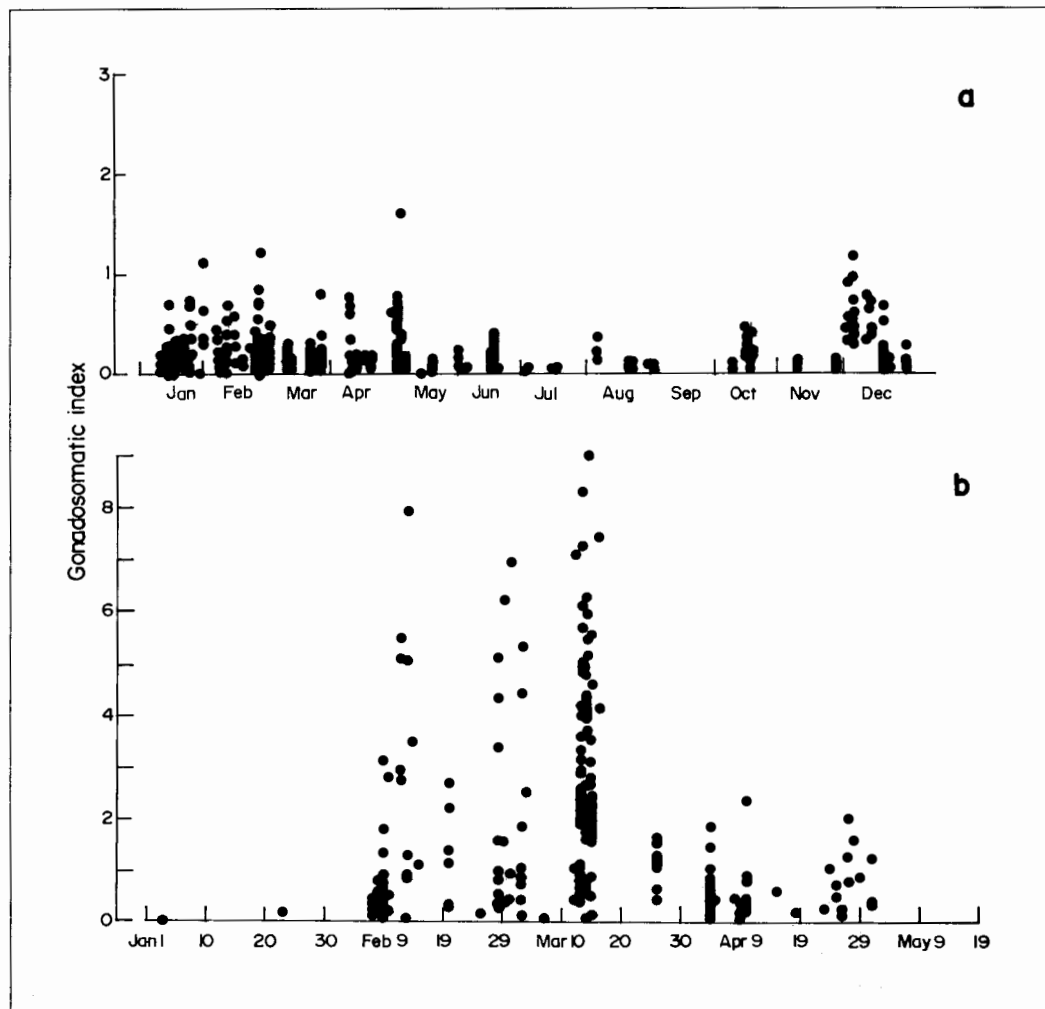
Fig. 1. Seasonal pattern of gonadosomatic indices of gag (*Mycteroperca microlepis*) **(a) 1991 data collected year-round in depths less than 50 m; (b) 1992 data collected during spawning season mostly from aggregation sites.** [*Patrón estacional de los índices gonadosomáticos del cuna aguají* (Mycteroperca microlepis) *(a) datos colectados a lo largo del año 1991 en profundidades menores a 50 m; (b) Datos colectados durante la estación de desove en 1992, mayormente de sitios de agregación.*]

fish collected over a broad geographic and temporal range (Koenig, unpubl.).

Spawning occurs on offshore reefs from southeast of Apalachicola to west of Tampa (and possibly further to the south) (Fig. 2). Spawning aggregations were concentrated at depths of about 80 m (range: 50 m to 120 m). GSIs of fish caught in shallow water (1992) were higher in February than in March, but GSIs of both groups (February and March) were much smaller than those recorded for gags captured at depths greater than 50 m (Fig. 3). During peak spawning, most mature females (i.e., >550 mm SL) caught at depths >50 m (Fig. 1b) had large, active gonads whereas those caught at the same time in shallower waters (<50 m) had relatively small gonads (Fig. 1a). Fish collected from spawning aggregations in March tended to be larger than fish collected

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Fig. 2. Dominant spawning grounds for gag (Myctero- perca microlepis) off the Gulf coast of Florida. [Campos de desove dominantes para el cuna aguají (Mycteroperca microlepis) fuera de las Costas del Golfo de Florida.]
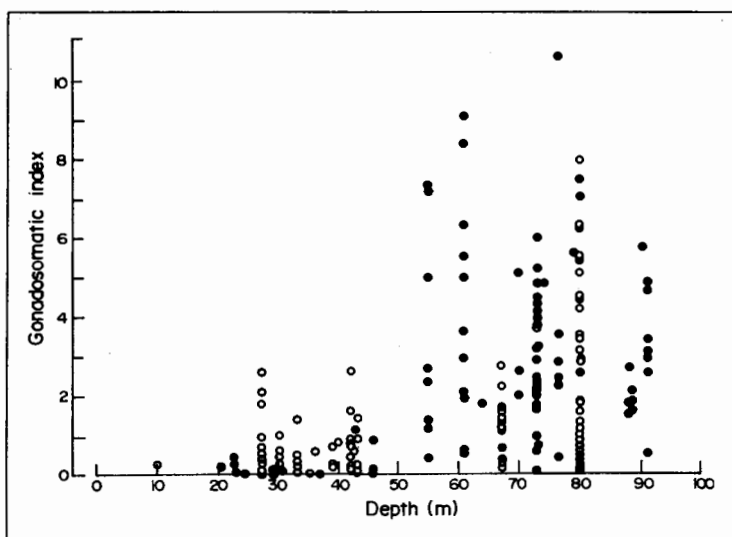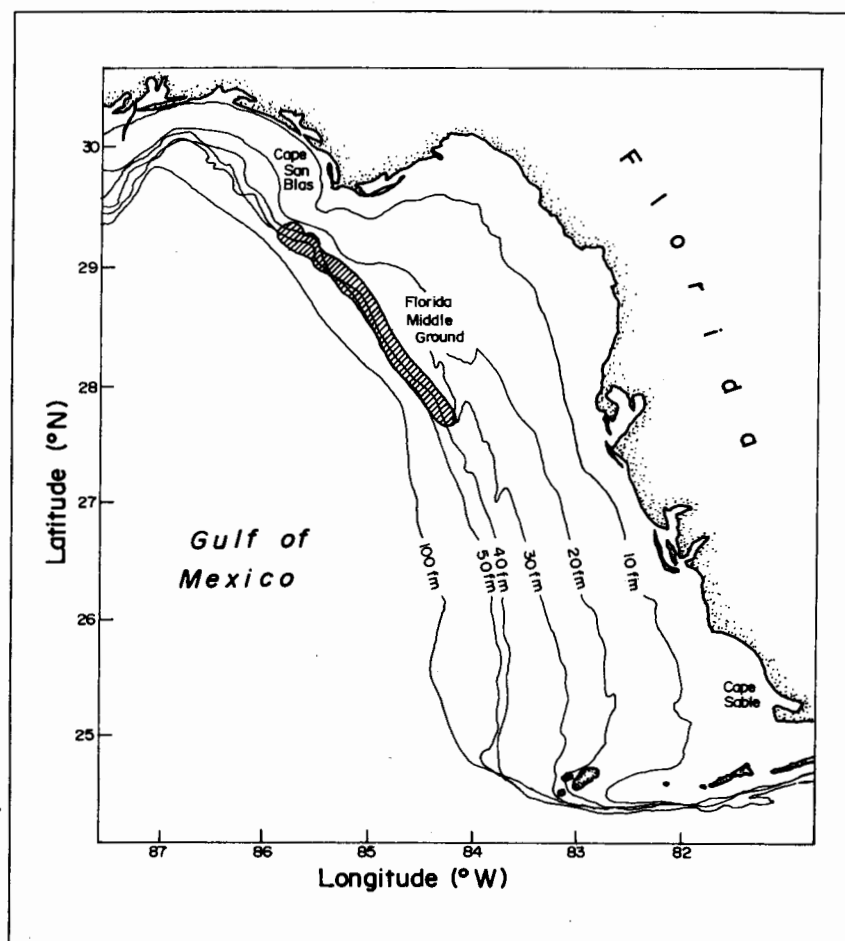

Fig. 3. Distribution of gonadosomatic indices relative to depth of capture for gag (Mycteroperca microlepis) during peak spawning (February = open circles; March = closed circles) in 1992. [Distribución de los índices gonadosomáticos en relación a la profundidad de captura del cuna aguají (Mycteroperca microlepis) durante el pico de desove (Febrero = círculos claros; Marzo = círculos obscuros) en 1992.]
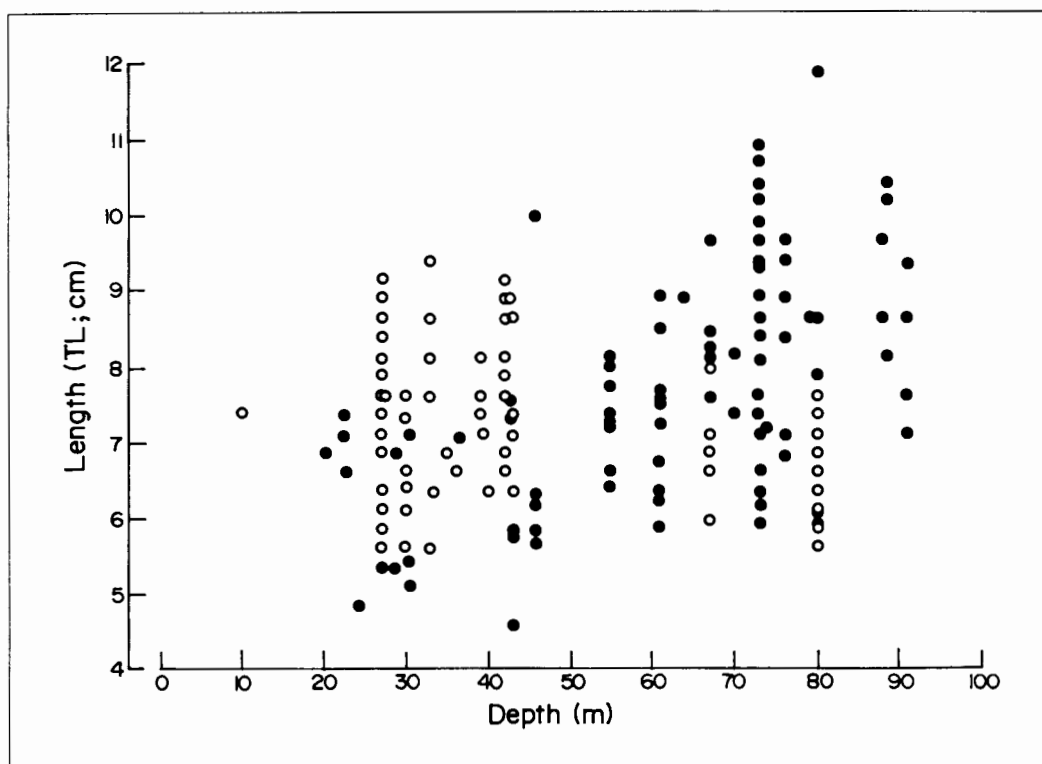
Fig. 4. Distribution of total length (cm) relative to depth of capture for gag *(Mycteroperca microlepis)* **during peak spawning (February = open circles; March = closed circles). [***Distribución de la longitud total (cm) en relación a la profundidad de la captura del cuna aguají* (Mycteroperca microlepis) *durante el pico de desove (Febrero= círculos claros; Marzo=círculos obscuros).***]**

in shallow (<50 m) water (Fig. 4), but this pattern appeared reversed in February.

Gonads examined histologically (N = 112) included 110 females, no males, and 2 transitionals. Nineteen of the fish were immature, 67 were inactive (47 mature, 20 uncertain), and 24 were mature and ripe. The inactive category includes fish that are clearly sexually mature but are not in spawning condition (N = 43) and fish for which level of maturity could not be determined. The smallest mature fish examined was 400 mm SL, 50% of the fish between 500 and 550 mm SL had matured, and 100% of the fish larger than 550 mm SL were mature.

The inactive gonads, most of which were collected from mature fish (N = 47) in shallow water (<50 m) during peak spawning periods, provide limited but highly suggestive

information about the spawning condition of females in shallow water. Spawning condition could be determined clearly in 15 of these fish: 10 (67%) showed no indication of either imminent or past spawning activity, 3 (20%) collected in February had developing oocytes suggesting a prespawning condition, and the remaining 2 (13%) collected in March were in postspawning condition. These data, combined with the data presented in Figs. 3 and 4, suggest that gags found in February in relatively shallow water consist of two types of mature females, those that will not spawn and those that will migrate to the spawning sites. In March, mature females in shallow waters consist of both nonspawners and those that have spawned and left the spawning sites.

Sex ratio and size frequency

The two data sets, historical and recent, show marked differences in both sex ratio and size frequency (Table 1). In both historical data sets the percentage of males among mature fish was 17%. The 95% confidence interval (binomial) for the historical Gulf data (13% to 21%) was narrower than the historical Atlantic data (11% to 23%) because of the smaller sample size of the latter. In the recent data sets, the percent males among mature fish was much lower, ranging from 2.7% to 1.3% (Table 1). The 95% confidence interval about the mean (2.2%) of the recent data sets was about 0.9% to 3.5%.

A comparison of the FSU-1991 size-frequency distribution and the FSU-1992 size-by-sex-frequency distributions with those of Hood and Schlieder (1992) (Fig. 5a and 5b, respectively) shows that a distinct loss of large fish has occurred over the 1980s (along with a reduction in the proportion and average size of males).

Fig. 6 shows size-by-sex-frequency distributions of data collected by NMFS (Panama City Laboratory) in 1991, 1992 and 1993. It shows a distinct reduction in average size compared with the historical data.

Transitionals were rare in all samples, historical and recent (Table 1). The size (mm TL) range of transitionals in the historical samples were: Gulf, 850 - 1 150 and Atlantic, 857 - 904. In the recent samples the size ranges of transitionals were: FSU-1992, 660 - 864; NMFS-1991, 725; NMFS-1992, 1 025 - 1 149; NMFS-1993, 525 - 1 175.

Gags have sexually dimorphic color patterns at least during the spawning season (Gilmore and Jones 1992). All of the large males we examined exhibited this pattern, which fishers have variously called "copperbelly", "charcoalbelly", or "rustybelly". Such pigment patterns persist even after capture. The smallest males in our sample apparently did not exhibit this pattern because they were not recognized as males until the gonads were examined microscopically. Only one male in the FSU-1992 collection (607 mm TL), was collected shallower than 50 m (29 m). In addition, the two smaller of the three FSU-1992 transitionals were collected shallower than 50 m.

We examined monthly variation in the average catch data for the Florida Gulf coast landings (1986-1992) and found that the highest catches occurred during the period immediately prior to, during and after peak

Table 1. Historical and recent sex ratio and size frequency of gag (*Mycteroperca microlepis*) (Pisces: Serranidae) in the eastern Gulf of Mexico. [*Proporción de sexos histórica y reciente, y frecuencia de tallas del cuna aguají* (Mycteroperca microlepis) *(Pisces: Serranidae) en el este del Golfo de México.*]

| Study	Collection dates	Collection areas	Males		Transitionals		Mature females		
			No.	%	No.	%	No.	%	Median sz
Hood and Schlieder (1992)	1977-1980	N.E. Gulf	134	17	6	0.8	659	82	850-900
Collins et al. (1987)	1977-1982	off South Carolina	51	17	4	1.3	253	82	800-850
Panama City Laboratory	1991	N.E. Gulf	12	2.7	1	0.2	427	97	800-849
	1992		8	2.5	2	0.6	309	97	750-799
	1993		8	1.3	2	0.3	613	98	700-749
FSU Laboratory	1992	N.E. Gulf	9	1.9	3	0.6	457	98	750-799
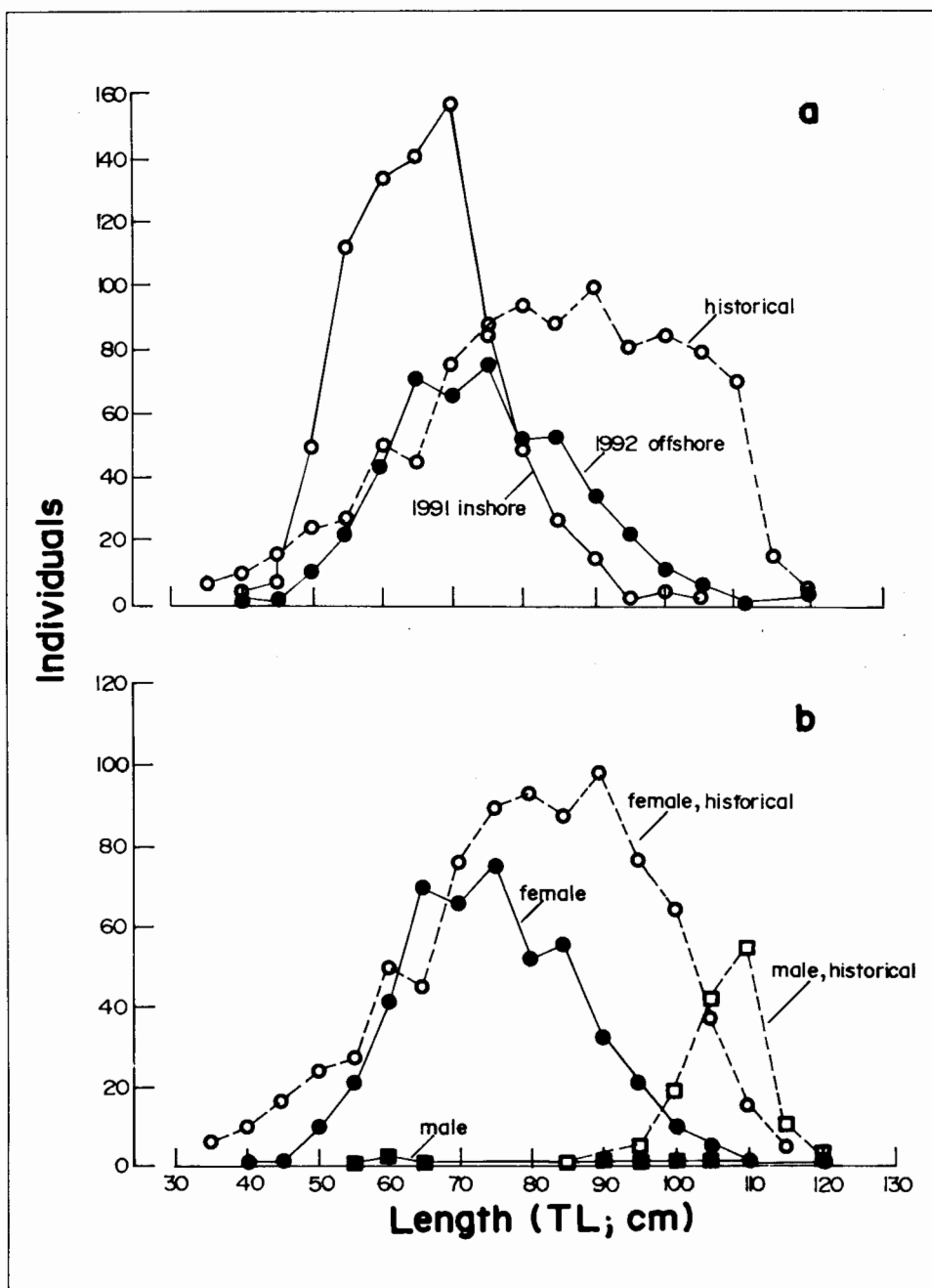
Fig. 5. (a) Size-frequency distributions for gag *(Mycteroperca microlepis)* **collected by FSU in 1991 (<50 m) and 1992 (>50 m) and by Hood and Schlieder (1992) in 1977-1980; (b) Size-frequency distributions by sex for gag** *(Mycteroperca microlepis)* **collected by FSU in 1992 (>50 m) and by Hood and Schlieder (1992) in 1977-1980.** [*(a) Distribución de frecuencia de tallas del cuna aguají* (Mycteroperca microlepis) *colectada por FSU en 1991 (<50 m) y 1992 (>50 m) y por Hood y Schlieder (1992) en 1977-1980; (b) Distribución de frecuencia por sexo para el cuna aguají* (Mycteroperca microlepis) *colectadas por FSV en 1992 (>50 m) y por Hood y Schlieder (1992) en 1977-1980.*]
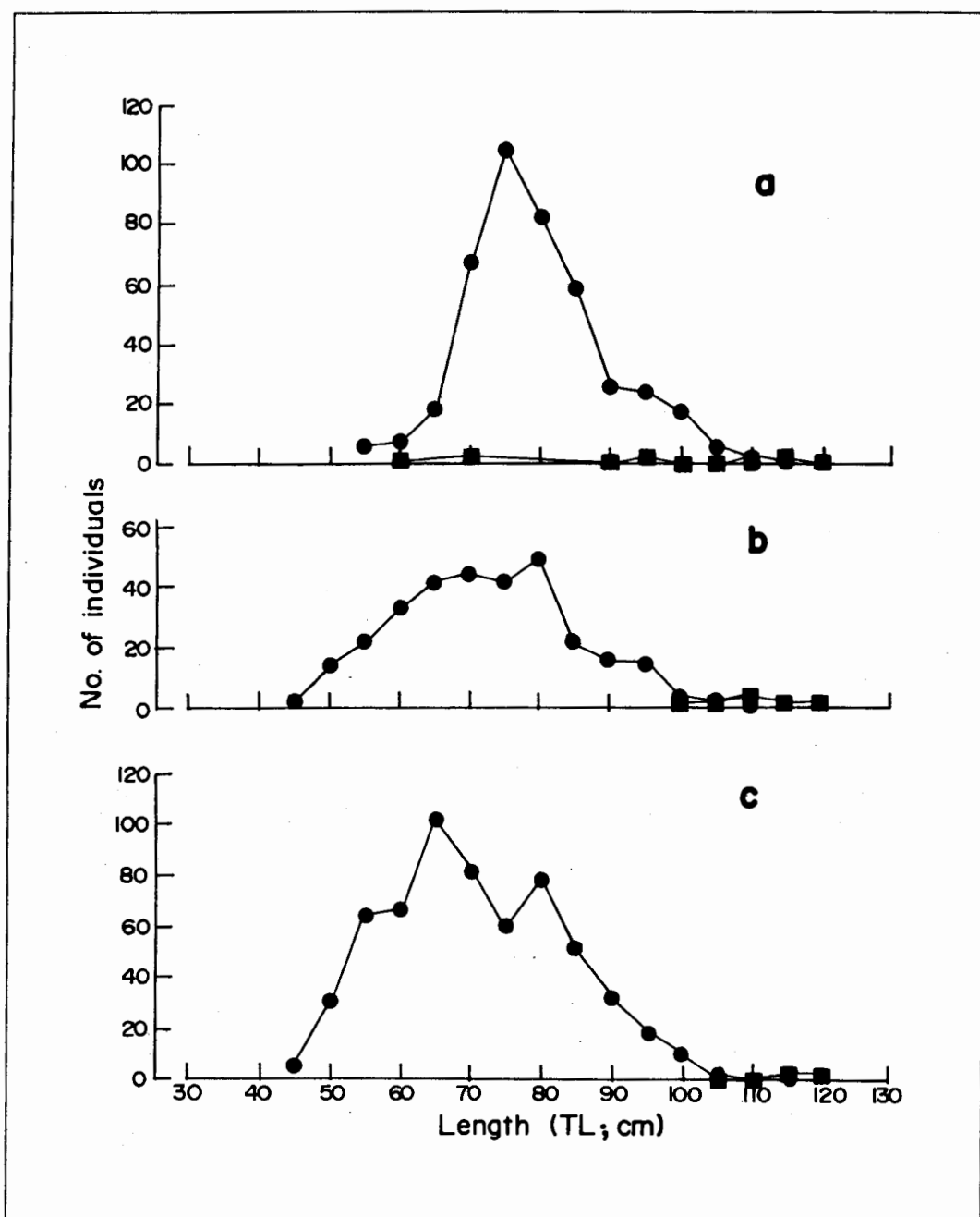
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Fig. 6. Size-frequency distributions by sex for gag (*Mycteroperca microlepis*), NMFS, Panama City Laboratory data: (a) 1991, (b) 1992, (c) 1993. [*Distribución de frecuencia por tallas por sexo para el cuna aguají* (Mycteroperca microlepis*), NMFS, datos de laboratorio de Panamá City: (a) 1991, (b) 1992, (c) 1993.*]

spawning (Fig. 7a). The mean number of trips was lowest during February and March, probably due to the high incidence of storms and danger associated with fishing these areas during that time of year (Fig. 7b). But clearly, the catch-per-unit effort (Fig. 7c) is highest exactly during peak spawning, indicating a high vulnerability of gags during this time.

Discussion

The peak spawning season in the Gulf population of gag is February through March and spawning aggregations occur in water depths from 50 to 120 m. Keener et al. (1988) showed similar spawning times for the Atlantic population of gags through the back-calculation of daily increments of juvenile otoliths, and Gilmore and Jones (1992) observed putative spawning aggregations within the same depth range as those in the Gulf off the east coast of Florida. Mitochondrial DNA analyses (Koenig and Ptacek, unpubl.) of Atlantic and Gulf populations of gags demonstrated a lack of genetic differentiation within and between populations. Thus, it appears that Atlantic and Gulf gag comprise a single genetic population with similar patterns of spawning and probably similar responses to exploitation. Burton (NMFS, Beaufort, unpubl.) showed that fishery landings of gag peaked during the time of gag spawning off the east coast of Florida. Although there are no recent studies of sex ratios of Atlantic gag, we found neither males nor transitionals in a sample (collected during the spawning season, 1993) supplied by commercial fishers (N = 170, Koenig, Coleman and Carr, unpubl.).

Several species of groupers have been shown to undergo annual migrations to well-defined spawning sites (Colin et al. 1987; Shapiro 1987; Waschkewitz and Wirtz 1990; Sadovy, in press). Van Sant et al. (1990) described a gag spawning migration

southwards to the east coast of Florida, based on tagging studies. Although no spawning migrations have been described for gag in the Gulf, they are implied from the consistent annual timing and location of the aggregations.

Gilmore and Jones (1992; pers. comm.) observed individual scamp returning to the same aggregation site in consecutive years. These investigators did not present direct observations of individual gag returning annually to the same sites, although they did observe consistent annual site-specific aggregations.

The occurrence of prespawning groups in gag has been observed and videotaped (D. DeMaria and W. Parks, commercial fishers, pers. comm.). Prespawning sites were observed by Parks to occur in shallow (20-40 m) water at annually consistent sites off the south Atlantic coast of Florida typically during late December or early January. The function of the prespawning groups is unknown.

Anecdotal accounts by commercial fishers indicate that gag spawning aggregations once exceeded the present range northward to more accessible locations southeast of Pensacola and throughout the Middle Grounds. Spawning sites are now restricted to the range depicted in Fig. 2. If gag aggregation sites are traditional and the northern aggregation sites have been depleted by fishing, then it is likely that continued aggregation fishing will eliminate other aggregation sites. Such a process may lead to fishery extinction, and this process is often cited as the cause for the collapses of other grouper fisheries (Olsen and Laplace 1979; Sadovy 1994).

Spawning has not been directly observed in gag; however, evidence presented by Gilmore and Jones (1992) suggests that gag form hierarchical spawning groups with single-male, multiple-female spawning events. Our data support his observation. Ripe testes from gag are relatively small and contain small amounts of milt which indicates single
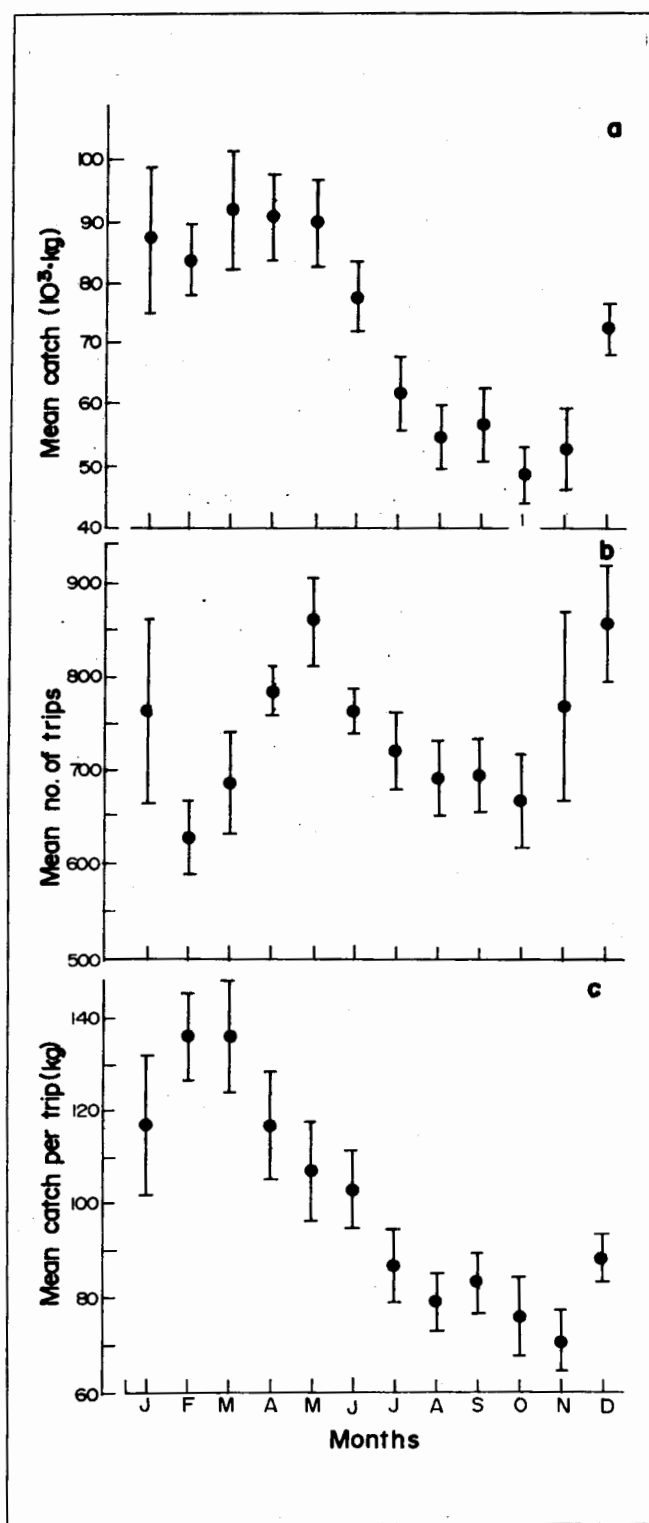
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Fig. 7. Florida Gulf coast landings of gag *(Mycteroperca microlepis)* from 1986 to 1992. (a) Mean monthly landings; (b) Mean monthly commercial grouper fishing trips; (c) Mean monthly catch per trip. [*Descargas en las costas del Golfo de Florida del cuna aguají* (Mycteroperca microlepis) *de 1986-1992. (a) Descarga media mensual; (b) Media mensual de viajes de pesca comercial del mero; (c) Media mensual de la captura por viaje.*]

male spawning (i.e., no sperm competition). Red hind (*Epinephelus guttatus*), also has single male spawning and males have small testes (Sadovy et al. 1994). In contrast, Nassau grouper (*Epinephelus striatus*) males, when ripe, have large, milt-filled testes and are multiple-male spawners (Colin 1992).

The proximal causes of sex change in groupers have important implications for fisheries management (Munro 1987). Management will be quite different for species in which sex change is age- or size-mediated (endogenous control, as suggested for gag by McErlean and Smith 1964) than for those exhibiting sociodemographic control (exogenous control, e.g., Shapiro 1987). To date, the only mechanism described for sex-changing reef fish species is sociodemographic control (Shapiro et al., in press).

The conditions of sex change (i.e., which fish changes sex and when) are determined in *Anthias squamipinnis*, a protogynous serranid (subfamily Anthiinae), by hierarchical associations within the social group (Shapiro 1981a). For example, removal of a territorial male from the group causes the dominant (= largest) female to change sex. It is possible that a similar process of sex change occurs in gag. Our size-by-sex-frequency data (Fig. 5b) support this contention, as no small males (<800 mm) occurred in historical samples, but were present in ours. That is, if the mechanism of sex change in gag is mediated by social or demographic factors, then smaller males and transitionals would be expected in the population as exploitation eliminated the larger size classes. However, our data do not support a hypothesis of sex change in gag which is determined by size alone.

The declines in average size and male:female sex ratios in the eastern Gulf of Mexico population of gag over the 1980s was coincident with increased fishing pressure (Ecklund 1993). Landings data for the Florida Gulf coast indicate that fishing pressure was most intense during the time of gag spawning aggregation formation (Gilmore and Jones 1992 and anecdotal information from fishers) and that the highest catch-per-effort occurs at the time of peak spawning (Fig. 7c). In addition, northwest Florida grouper fishers report that they have experienced a steady decline in gag landings over the last 12 years. Unfortunately, stock declines cannot be verified because before 1986 all Gulf groupers were lumped in the landings data. It appears likely that, in addition to general stock declines due to heavy fishing pressure, population-level size- and sex-ratio changes are the direct result of fishing activities on the spawning aggregations. This contention is supported by the observations of Gilmore and Jones (1992 and pers. comm.), who reported that hook-and-line fishing on gag (and scamp) spawning aggregations tended to select males before females. If fishing selection for males occurs, then hook-and-line estimates of sex ratio (Table 1) actually overstimate the actual (absolute) proportion of males.

Although males may be selected by hook-and-line fishing, this observation alone does not explain how aggregation fishing could override compensatory sex-change mechanisms and reduce the proportion of male gags. If compensatory sex change mechanisms were operational in the male-deficient population, an increase in the proportion of transitionals would be expected. However, the proportion of transitionals is about the same in both historical and contemporary samples (Table 1). This observation could be explained if transitionals were also selected by fishing. Shapiro (1981b) and others have shown that among protogynous species individuals induced to undergo sex change rapidly adopt stereotypic male behaviors before they become functional males. The time necessary to complete transition in gag is unknown; however, data from artificial induction of sex change (Roberts and Schlieder 1983) suggest that it may take months.

Nevertheless, if fishing selection of males is based on male behavior, as Gilmore and Jones (1993) suggest, then transitionals, once they adopt male behaviors, will also be selected by fishing.

Selection of male and transitional gags in spawning aggregations should cause a depression of the male:female ratio, but when aggregations disperse and fishing pressure is lessened at nonspawning times of the year it would seem that the opportunities for sex change would increase. Therefore, if sex change could be induced at all times of the year, a higher frequency of males and/or transitionals would be expected in the population during nonspawning times. This increase in males (and/or transitionals) should be reflected in the catch at the beginning of the spawning season. However, no such increases in males nor transitionals were observed. If, on the other hand, males and females were segregated during nonspawning times of the year, the only opportunity for female "assessment" of the altered sex ratio would occur when the two sexes reunited at the time of spawning. Shapiro et al. (in press) described a similar system of sex segregation in the red hind and discussed possible mechanisms which could account for the lack of sex change among all-female groups during nonspawning times. Anecdotal evidence suggests that large male gags remain offshore; commercial fishers say that it is rare to catch large males that are distinctively colored ("copperbellies") in water shallower than 40 m. Our data support this contention, but the possibility of males lacking characteristic color patterns exists in our data set. Clearly, the temporal and spatial distribution of males needs further investigation. Assuming that males remain offshore throughout the year and females disperse after spawning to inshore sites (and sex change is socially mediated), then sex change would likely be initiated only at the time of spawning. It is possible that prespawning aggregations play a role

in sex change, but these ephemeral aggregations are completely unstudied.

Selection of males and transitionals from spawning aggregations could explain the relatively rapid depletion of large adults from the Gulf population of gag. The largest fish in the population are in the spawning aggregations and the largest individuals of each spawning aggregation are males, transitionals and dominant females. Removal by fishing of the males and transitionals presumably induces sex change in the dominant females, then these too are selected. Although size reduction in exploited fish populations is a general phenomenon (Bohnsack 1989) based on increased probability of capture with age (size), it would probably not act as rapidly as the direct removal of the largest individuals.

Several points are important to consider in relation to the comparison of historical and recent data sets. Although random sampling cannot be assumed for the overall data sets, bias would be minimized if the data were stratified by season and depth because large gag and males tend to occupy deeper water, especially during the spawning season. Thus, our 1991 size-class data are biased towards the smaller sizes of adult gags because samples were taken from shallow water. By contrast, our 1992 size-class data are biased towards larger sizes (and probably a high male:female sex ratio) because most of the samples came from deepwater during the spawning season. It is likely that historical samples were not taken from spawning aggregations because the GSIs were relatively small during the spawning season (Hood and Schlieder's mean peak GSI value was less than 2.0). Thus, our 1991 and 1992 data sets bracket the 'true' population size frequency (Fig. 5a) and the 1992 data set is biased in favor of a higher male:female sex ratio. In addition, the data set collected by the NMFS Panama City Laboratory had an additional bias toward more males because

"copperbellies" were selected from the catch (at the fish house) before the catch was sampled. Thus, males are probably even rarer in the population than our data indicate.

The question remains: What does a reduced proportion of males in the gag population mean in terms of reproductive capacity and ultimately recruitment? Intuitively, fewer males than is evolutionarily adaptive for a particular mating system would seem to restrict spawning opportunities for females in that system. As far as we know, there is a complete lack of information on this subject, except for the simulation models of Bannerot (1984) which compared the response, in terms of reproductive capacity, of the gonochorist and protogynist reproductive modes at various levels of exploitation. Bannerot found protogynists generally superior to gonochorists in reproductive capacity; however, under reduced male:female sex ratios the reproductive capacity of the protogynists dropped precipitously. Clearly, the relationship of sex ratio to reproductive capacity (and/or recruitment) needs to be examined in detail.

The response of gag to fishing pressure serves as an example of the importance to fishery management of knowledge of the details of reproductive strategies of exploited species. Even within the protogynous hermaphroditic mode of reproduction there may be widely different responses to fishing pressure, especially if that pressure is applied to the spawning fish. For example, we compared red grouper size-by-sex ratios of fish collected in the early 1960s (N = 594, Moe 1969) with our red grouper collections of 1991 and 1992 (N = 450, unpublished data). Both data sets were collected in a similar manner and in overlapping areas. We found no significant difference in size distribution or in sex ratios (22% males [plus transitionals] in Moe's sample and 24% males [plus transitionals]

in ours) even though red groupers are subject to exploitation rates at least as great as those of gags and at all times of the year (Goodyear and Schirripa 1993).

Effective management depends on detailed information concerning the complex life histories of exploited species at many levels of biological organization. Such detailed information is difficult, time consuming, and expensive to gain. An immediate management measure for gag, given the evidence presented in this paper on the effects of fishing spawning aggregations, should involve closure of either the spawning areas or season. Before, during and after the closure, gag should be monitored for sex ratio, gonad condition (e.g., rates of atresia) and recruitment success (Koenig and Colin, in press). If our hypotheses are correct about the timing and nature of gag sex change induction and fishing selection then the proportion of males should rise the second year after fishing of spawning aggregations stops.

Acknowledgements

References

Bannerot, S.P. 1984. The dynamics of exploited groupers (Serranidae): an investigation of the protogynous hermaphroditic reproductive strategy. University of Miami, Coral Gables, Florida. 392 p. Ph.D. dissertation.

Bannerot, S.P., W.W. Fox and J.E. Powers. 1987. Reproductive strategies and the management of snappers and groupers in the Gulf of Mexico and Caribbean, p. 295-327. In J.J. Polovina and S. Ralston (eds.) Tropical snappers and groupers: biology and fisheries management. Westview Press, Boulder.

Bohnsack, J.A. 1989. The potential of marine fishery reserves for reef fish management in the US Southern Atlantic. NOAA Tech. Mem. NMFS-SEFC-261, 40 p.

Bullock, L.H. and G.B. Smith. 1991. Seabasses (Pisces: Serranidae). Memoirs of the Hourglass Cruises VIII (II), 243 p.

Colin, P.L. 1992. Reproduction of the Nassau grouper, Epinephelus striatus (Pisces: Serranidae) and its relationship to environmental conditions. Env. Biol. Fish. 34:357-377.

Colin, P.L., D.Y. Shapiro and D. Weiler. 1987. Aspects of the reproduction of two groupers, Epinephelus guttatus and E. striatus, in the West Indies. Bull. Mar. Sci. 40:220-230.

Collins, M.R., C.W. Waltz, W.A. Roumillat and D.L. Stubbs. 1987. Contribution to the life history and reproductive biology of gag, Mycteroperca microlepis (Serranidae) in the South Atlantic Bight. US Fish. Bull. 85:648-653.

Ecklund, A.M. 1993. A literature review of the gag grouper, Mycteroperca microlepis. National Marine Fisheries Service, SE Fisheries Science Center, Miami. Contribution MIA 92/93-72.

Gilmore, R. G. and R. J. Jones. 1992. Color variation and associated behavior in the epinepheline groupers, Mycteroperca microlepis (Goode and Bean) and M. phenax Jordan and Swain. Bull. Mar. Sci. 51(1):83-103.

Goodyear, C.P. and M.J. Schirripa. 1993. The red grouper fishery of the Gulf of Mexico. National Marine Fisheries Service, SE Fisheries Science Center, Miami Contribution MIA-90/91-86.

Hood, P.B. and R.A. Schlieder. 1992. Age, growth and reproduction of gag Mycteroperca microlepis (Pisces: Serranidae), in the eastern Gulf of Mexico. Bull. Mar. Sci. 51(3):337-352.

Huntsman, G.R. and J.R. Waters. 1987. Development of management plans for reef fishes-Gulf of Mexico and US South Atlantic, p. 533-560. In J.J. Polovina and S. Ralston (eds.) Tropical snappers and groupers: biology and fisheries management. Westview Press, Boulder.

Keener, P., G.D. Johnson, B.W. Stender, E.B. Brothers and H.R. Beatty. 1988. Ingress of postlarval gag, Mycteroperca microlepis (Pisces: Serranidae) through a South Carolina barrier island inlet. Bull. Mar. Sci. 42(3):376-396.

Koenig, C.C. and P.L. Colin. Absolute abundance, and survival of juvenile gag grouper, Mycteroperca microlepis, in seagrass beds of the northeastern Gulf of Mexico. Proc. Gulf Caribb. Fish. Inst. 45. (In press).

Link, G.W., Jr. 1980. Age, growth, reproduction, feeding, and ecological observations on the three species of Centropristis (Pisces: Serranidae) in North Carolina waters. The University of North Carolina, Chapel Hill. 277 p. Ph. D. dissertation.

McErlean, A.J. and C.L. Smith. 1964. The age of sexual succession in the protogynous hermaphrodite Mycteroperca microlepis. Trans. Am. Fish. Soc. 93(3):301-302.

Moe, M.A., Jr. 1969. Biology of the red grouper (Epinephelus morio Valenciennes) from the eastern Gulf of Mexico. Prof. Pap. Ser., Fla. Mar. Lab, 10, 95 p.

Munro, J.L. 1987. Workshop synthesis and directions for future research, p. 639-659. In J.J. Polovina and S. Ralston (eds.) Tropical snappers and groupers: biology and fisheries management. Westview Press, Boulder.

Olsen, D.A. and J.A. Laplace. 1979. A study of a Virgin Islands grouper fishery based on

a breeding aggregation. Proc. Gulf Carib. Fish. Inst. 31:130-144.

Roberts, D.E., Jr. and R.A. Schlieder. 1983. Induced sex inversion, maturation, spawning, and embryogeny of the protogynous grouper, *Mycteroperca microlepis*. J. World Maricult. Soc. 14:639-649.

Sadovy, Y. 1994. Grouper stocks of the Western central Atlantic: the need for managment and management needs. Proc. Gulf Caribb. Fish. Inst. 43:43-64.

Sadovy, Y. The case of the disappearing grouper: *Epinephelus striatus*, the Nassau grouper, in the Caribbean and Western Atlantic. Proc. Gulf Caribb. Fish. Inst. 45. (In press).

Sadovy, Y., P.L. Colin and M.L. Domeier. 1994. Aggregation and spawning in the tiger grouper, *Mycteroperca tigris* (Pisces: Serranidae). Copeia: 511-516.

Shapiro, D.Y. 1981a. Size, maturation and the social control of sex reversal in the coral reef fish *Anthias squamipinnis*. J. Zool. Lond. 193:105-128.

Shapiro, D.Y. 1981b. Behavioural changes of protogynous sex reversal in a coral reef fish in the laboratory. Anim. Behav. 29:1185-1198.

Shapiro, D.Y. 1987. Reproduction in groupers, p. 295-327. In J.J. Polovina and S. Ralston (eds.). Tropical snappers and groupers: biology and fisheries management. Westview Press, Boulder.

Shapiro, D.Y., G. Garcia-Moliner and Y. Sadovy. Social system of an inshore sub-population of the red hind grouper, *Epinephelus guttatus* (Pisces: Serranidae). Env. Biol. Fish. (In press).

Van Sant, S.B., M.R. Collins and G. Sedberry. 1990. Preliminary evidence from a tagging study for a gag (*Mycteroperca microlepis*) spawning migration with notes on the use of oxytetracycline for chemical tagging. Proc. Gulf Caribb. Fish. Inst. 43:417-428.

Waschkewitz, R. and P. Wirtz. 1990. Annual migration and return to the same site by an individual grouper, *Epinephelus alexandrinus* (Pisces: Serranidae). J. Fish Biol. 36(5):781-782.

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Proceedings of an EPOMEX/ICLARM International Workshop
on Tropical Snappers and Groupers
held at the University of Campeche
Campeche, Mexico
26-29 October 1993

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ICLARM

International Center for Living Aquatic Resources Management

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